

LATE TERTIARY HYAENIDAE FROM LANGEBAANWEG, SOUTH AFRICA, AND THEIR RELEVANCE TO THE PHYLOGENY OF THE FAMILY

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(With 11 figures and 4 tables)

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ABSTRACT

The Hyaenidae are divided on phylogenetic grounds into the 'Hyaena group' and the 'Percrocuta group', both of which are represented by fossil forms from the latest Miocene/early Pliocene Varswater Formation at Langebaanweg, South Africa, four species being assigned to the *Hyaena* group and one to the *Percrocuta* group. The latter species is *Adcrocuta australis*, while the others are *Ictitherium preforfex*, *Hyaena abronia*, *Hyaenictitherium namaquense* and an unnamed species of *Euryboas*. They reflect a pattern of representation established during the late Miocene, although individual species are more advanced than their Eurasian late Miocene counterparts, and they fill an important temporal gap in the recorded history of the family. *Chasmaporthetes* is regarded as a member of the *Percrocuta* group and not as a close relative of *Euryboas*.

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INTRODUCTION

There are only four hyaenid species still extant and they comprise a relatively uncommon element in the faunas of Africa and southern Eurasia. The species are the striped hyaena (*Hyaena hyaena*), the brown hyaena (*Hyaena brunnea*), the spotted hyaena (*Crocuta crocuta*) and the aardwolf (*Proteles cristatus*). The latter is an aberrant insectivorous species, while the others are well adapted to a scavenging role, although they may also be actively predacious.

The family, which stemmed from the Viverridae during the Miocene, was formerly more diverse and widespread, and, although hyaenas are rare as fossils in North America, they are sometimes abundantly represented in late

Cenozoic deposits in the Old World. In spite of this, opinions on hyaenid inter-relationships and phylogeny are almost as numerous as papers dealing with these subjects, some recent examples being Thenius (1966), De Beaumont (1967), Ficarelli & Torre (1970), Hendey (1974a), Schmidt-Kittler (1976), and Galiano & Frailey (1977). There is, however, one important point about which there does appear to be general agreement. Evidently hyaenids evolved from viverrids on more than one occasion, and on phylogenetic grounds the family is divisible into at least two major groups. These two groups have yet to be accorded formal nomenclatural recognition, and they are here informally termed the '*Percrocuta*' and '*Hyaena*' groups.

The former was the first to be differentiated, having evolved from an as yet undetermined viverrid ancestor (or ancestors) early in the Miocene. The genera (or subgenera) constituting this group are *Percrocuta*, *Dinocrocuta* and *Adcrocuta* (see Schmidt-Kittler 1976). For reasons which will be explained later, the genus *Chasmaporthetes* is also included here. Members of the group appear in Africa and Eurasia as progressive hyaenas late in the middle Miocene. They may have had their origins in Africa where the Miocene fossil record is comparatively poor. Certainly the superior Eurasian record includes no appropriate links with the Viverridae.

By contrast, the evolution of the *Hyaena* group is well documented by Eurasian fossils. The stem genera were the 'Vindobonian' *Protictitherium* and *Miohyaena* (Schmidt-Kittler 1976), which were apparently descended from the late Oligocene *Herpestides* (De Beaumont 1967). The group radiated during the late Miocene and a number of small- to medium-sized species occurred together as a characteristic element in Eurasian '*Hipparion* faunas' (i.e. Turolian in Europe and Turolian equivalent in Asia). There is as yet no consensus on the nomenclature of the late Miocene taxa. The genera recognized here are *Plioviverrops*, *Ictitherium*, *Palhyaena*, *Hyaenictitherium*, *Hyaenictis*, and *Lycyaena*. Numbers of species and subspecies have been named, but the complexities of the situation will not be explored.

Many of the recorded late Miocene hyaenids of Eurasia were separated from one another temporally and/or geographically, but there are well-documented examples of the contemporary occurrence of several species at a single locality. Pikermi in Greece is perhaps the most extreme case, its fauna including five members of the *Hyaena* group (i.e. *Plioviverrops orbigny*, *Ictitherium robustum*, *Palhyaena hipparionum*, *Hyaenictis graeca*, and *Lycyaena chaeretis*), and a percrocuta (*Adcrocuta eximia*) (Pilgrim 1931). A similar association is evident at several localities in China, where there are three *Hyaena* group species (*Ictitherium gaudryi*, *Palhyaena wongii*, and *Hyaenictitherium hyaenoides*), and a percrocuta (a variety of *A. eximia*) (Zdansky 1924; Kurtén 1953).

The diversity of hyaenids in Eurasia during the late Miocene is a reflection of the wealth of the fauna as a whole at that time. It is a period of which Kurtén (1971: 135) has said 'may well be regarded as the climax of the entire Age of

Mammals'. This probably applies in the case of Africa as well, but the late Miocene fauna of the continent is not well known.

It is, however, becoming increasingly clear that African faunas of the very late Miocene and early Pliocene were as spectacular in character as the Eurasian 'Hipparion faunas', which predate them. The African faunas in question include those from Mpesida (Bishop *et al.* 1971), Lothagam 1 (Smart 1976), Lukeino (Pickford 1975), Sahabi (Petrocchi 1952), 'E' Quarry at Langebaanweg (Hendey 1976) and Kanapoi (Behrensmeyer 1976). Smart (1976) has already pointed out that climatic and environmental changes, which adversely affected Eurasian faunas towards the end of the Miocene, had less of an impact in Africa. Indeed, they may have had the effect of increasing mammalian migration from Eurasia to Africa.

In spite of the improving situation in Africa, the very late Miocene/early Pliocene fossil record in the Old World is generally poor. This was a period for which recorded fossil occurrences are few in number, widely dispersed and have often yielded faunas of limited size. There is a considerable improvement in the record throughout the Old World during the late Pliocene, a tendency which continues into the succeeding Pleistocene epoch.

The Old World late Tertiary record is thus characterized by both temporal and geographical irregularities, which complicate interpretations of the origins and history of mammals that lived during this period. The problem is particularly acute in the case of those mammalian groups, such as the Hyaenidae, which were both diverse and widespread. Consequently any fossil occurrence which dates from a poorly known part of the record, and which produces good samples of material, could make a significant contribution towards the understanding of the history of such groups.

'E' Quarry at Langebaanweg is an occurrence of this kind. Deposits exposed in this quarry are comprised largely of the latest Miocene/early Pliocene Varswater Formation, which has produced a fossil assemblage of size and diversity unequalled by contemporary occurrences elsewhere in Africa (Hendey 1976). One of the more remarkable features of this fauna is the number and variety of carnivores which are represented (Hendey 1974*a*, 1976, 1977), and, of the terrestrial species, Hyaenidae occur most commonly. At least five hyaenid species are represented, which is in marked contrast to the situation at other late Miocene/early Pliocene localities in Africa (Table 1).

Before proceeding to an account of the hyaenids, a few further observations on the 'E' Quarry fauna and deposits are necessary to place them in perspective.

Evidence which indicates an early Pliocene age for the Varswater Formation was recently reviewed (Hendey 1978: 2). The dating of this formation is based on comparisons between certain of its taxa with their counterparts in the east African sequence, for which there are some radiometric dates. The suggested age limits of 4 to 5 million years (m.y.) for the Varswater Formation are, however, not securely established. The 4 m.y. limit has already been questioned (Hendey 1978), and there is now reason to believe that the older limit may have

TABLE 1
Late Miocene/early Pliocene Hyaenidae of Africa.

LOCALITY	AGE	TAXA	REFERENCES
Kanapoi	early Pliocene	<i>Hyaena</i> sp.	Behrensmeyer 1976
Langebaanweg (‘E’ Quarry)	latest Miocene/ early Pliocene	<i>Ictitherium preforfex</i> <i>Hyaena abronia</i> <i>Hyaenictitherium namaquense</i> <i>Euryboas</i> sp. <i>Adrocuta australis</i>	This report
Sahabi	late Miocene or early Pliocene	Hyaenidae gen. et sp. indet.	—
Lukeino	late Miocene	cf. <i>Crocota</i> sp.	Pickford 1975
Lothagam 1	late Miocene	aff. <i>Euryboas</i> sp.	Smart 1976

been underestimated. This matter will be dealt with in detail elsewhere, but in the meantime the former practice of referring to the age of the Varswater Formation and its fossils as ‘early Pliocene’ is here replaced by the reference, ‘latest Miocene/early Pliocene’.

It is nevertheless perfectly clear that the Varswater Formation fauna as a whole postdates the classic Eurasian late Miocene faunas such as those from Pikermi and lower Samos, which are between 7 and 10 m.y. old, but predates the Old World late Pliocene/early Pleistocene faunas, which are younger than 3,5 m.y. In other words, it dates from a period towards the end of the Tertiary when the Old World fossil record is generally poor.

Another important point about the Langebaanweg (‘E’ Quarry) fauna relevant to the present study is that it comes from the most southerly part of Africa and is thus geographically far removed from those faunas with which it is here compared and contrasted. It is therefore possible that the ‘E’ Quarry fauna, like that of the near-by Baard’s Quarry, includes regional variants of more widespread taxa, endemic taxa and even late surviving members of lineages which were elsewhere extinct (Hendey 1978). If there are regional peculiarities in the fauna and these are not recognized, this could result in incorrect interpretations of the relationships of such taxa. Furthermore, the populations to which the Langebaanweg species belonged were probably not directly ancestral to later ones elsewhere.

The Cenozoic terrestrial faunas of the most southerly parts of Africa may characteristically have contributed little in the way of emigrants to regions further north. Instead the composition of the local faunas is likely to have been changed largely by immigration from the north and some endemic speciation, while local extinctions were not necessarily coincident with those elsewhere. The region may thus be viewed as a terminus in a zoogeographic sense. Nevertheless, local populations may have exhibited all the characteristics of their more northerly counterparts from which subsequent populations did evolve. Thus,

when Langebaanweg species are suggested as ancestors of later ones, they were themselves not directly ancestral, but simply represent the kinds of animals from which later ones were derived (i.e. 'structural ancestors').

The observations in the preceding paragraphs are conveniently summarized if the Langebaanweg ('E' Quarry) fauna is visualized as a younger southern African counterpart of the classic '*Hipparion* faunas' of Eurasia. It differs from such faunas because it is separated from them by the width of a continent and a few million years in time. In spite of this, its composition is of an essentially similar pattern. The 'E' Quarry fossil assemblage, with its eighty mammalian species, provides the best evidence yet that the Old World late Tertiary 'climax of the entire Age of Mammals' persisted over much, if not all, of Africa long after it had passed in Eurasia.

A final point about the 'E' Quarry fauna relevant to the present report is that it includes species from a variety of habitats (Hendey 1976: 222-230). As a general rule terrestrial carnivores such as hyaenids are not as tied to particular habitats as are, for example, herbivores such as bovids. However, the contemporary occurrence at Langebaanweg of several closely related hyaenids suggests that the species concerned did occupy different habitats. A similar association of three hyaenid species in China during the late Miocene led to the suggestion by Kurtén (1953: 45) that one was a 'steppe form', one a 'forest form', and the third an 'intermediate'.

The situation at Langebaanweg, and indeed elsewhere, cannot be completely explained by habitat preference, since there were more hyaenid species than major habitat types. The co-existence of more than one species in a given environment is made possible by different behaviour patterns in the species concerned. This no doubt applies in the case of certain of the Langebaanweg hyaenids, but the habitat preference factor is almost certainly significant as well, since certain species occur commonly in, or are restricted to, deposits of particular kinds (e.g. river channel, floodplain). It is thus possible that while some species lived in the immediate vicinity of what was then a river estuary, others lived further inland and the remains of individuals were transported to the area of deposition by the river. While it is not possible to relate individual species to major habitat types (e.g. riverine woodlands, open plains), it is nevertheless significant that elements of the faunas from such habitats were incorporated in the Varswater Formation.

To sum up, the 'E' Quarry fossil occurrences are a potentially important source of information on Hyaenidae for the following reasons:

1. the fauna dates from a period which has a comparatively poor fossil record in the Old World;
2. the occurrences are situated on a continent for which the whole late Tertiary record is poor, but which may well have played a more important role in hyaenid evolution than has hitherto been supposed;
3. the sample sizes of individual taxa are reasonably good;
4. elements from more than one major habitat type are included in the fauna.

THE LANGEBAANWEG HYAENIDAE

INTRODUCTION

Five hyaenid species were described in a recent study of material from 'E' Quarry (Hendey 1974a). They were identified as follows: *Hyaenictis preforfex*, *Hyaena abronia*, *Hyaena* sp. B, *Hyaena* sp. E, and *Percrocuta australis*.

Hyaena sp. E is known only from a mandible fragment of an immature individual and, since its status is uncertain, it is excluded from the discussions which follow. Each of the remaining four species is known from cranial remains of three or more individuals and incomplete postcranial skeletons of at least two individuals. In addition, there is one undescribed species, a *Euryboas*, which is represented by the cranial remains of several individuals and an incomplete postcranial skeleton of one individual. The present situation in respect of individual species is now reviewed.

The smallest of the Langebaanweg hyaenids, that identified previously as *Hyaenictis preforfex*, has proved to be a problematical species. The type specimen is the damaged skull and incomplete postcranial skeleton of an aged individual (Hendey 1974a) from bed 3aS of the Pelletal Phosphorite Member (Hendey 1976: 226–230, 1978: 3). Additional specimens assigned to this species have since been found in bed 3aN of the same member and, although of comparable size, the new specimens differ from the holotype in certain dental characters. The differences are here regarded as more apparent than real and are ascribed to the aged condition of the holotype. Certain of the characteristics of the species mentioned in this report are evident in the bed 3aN sample but not in the holotype. They include a prominent M_1 metaconid, a feature which suggests that the genus concerned was not *Hyaenictis*. The reassessment of this species also suggests that it may not have been ancestral to the Transvaal '*Hyaenictis*' *forfex* as indicated earlier.

The additional '*Hyaenictis*' *preforfex* specimens show that this species was more similar to the second of the Langebaanweg hyaenids, *Hyaena abronia*, than had previously been supposed. Specimens which are unequivocally assigned to *H. abronia* are from the Quartzose Sand Member, which underlies the Pelletal Phosphorite Member, and are from floodplain deposits, whereas all the '*H.*' *preforfex* specimens are from river channel deposits. *H. abronia* is perhaps the least problematical of the Langebaanweg hyaenids in terms of its status and relationships.

The third, and next largest, of the species is the unnamed *Hyaena* sp. B, which is known only from the floodplain deposits of the Quartzose Sand Member. At least two additional individuals of this species are now represented and there is no longer any doubt that it is distinct from *H. abronia*. The possibility that species B and the poorly known '*Hyaena*' *namaquensis* from Kleinzee (Stromer 1931) were closely related was mentioned earlier (Hendey 1974a: 147). The additional species B specimens have made a close relationship seem more than just possible. The only observable difference between '*H.*' *namaquensis* and

species B is that the M_1 of the former is slightly longer and narrower. In spite of this, species B is here identified with '*H.*' *namaquensis* since the small M_1 size difference is outweighed by the general size similarity, comparable tooth morphology, the proximity of the Langebaanweg and Kleinzee occurrences and the likelihood that they are broadly contemporaneous.

Many of the specimens belonging to the three species already mentioned were excluded from the present study because the general similarity in the characteristics of the species creates the potential for incorrect identification. Only the best preserved and most complete specimens, that is, those which undoubtedly belong to the species concerned, were taken into account. In addition, each sample was limited to specimens from a single stratigraphic unit. The specimens examined were as follows:

'*Hyaenictis*' *preforfex*—7 individuals from bed 3aN of the Pelletal Phosphorite Member (SAM-PQ-L33046, L31028, L31333, L32893, L33520, L33842, L34778).

Hyaena abronia—4 individuals from the Quartzose Sand Member (L14186, L20984, L21009, L22202).

'*Hyaena*' *namaquensis*—3 individuals from the Quartzose Sand Member (L12848, L21008, L25026).

These three species are clearly closely related members of the *Hyaena* group and are distinguished from one another principally on the basis of size. They are characterized by the presence of P_1 and M_2^2 , although M^2 is sometimes absent in *H. abronia*, and are generally similar in terms of tooth morphology (Figs 1–2).

The fourth species is the undescribed *Euryboas*. It is similar in overall size to '*H.*' *namaquensis*, but is distinguished by the absence of P_1 , the occasional absence of M_2 , shorter M^1 , reduction or loss of the M_1 metaconid, smaller and simpler M_1 talonid and longer but narrower P_2^2 to P_4^4 and M_1 (Fig. 6, Table 2). The Langebaanweg *Euryboas*, which is apparently the earliest and most primitive known member of the genus, will be fully described elsewhere. Remains of only two individuals were taken into account in the present study (L21000, L21788). Both are from deposits in the Quartzose Sand Member which were probably laid down close to, or even in, a river channel. Other specimens probably belonging to this species are from river channel deposits of the Pelletal Phosphorite Member.

The fifth and largest of the 'E' Quarry hyaenids is a member of the *Percrocuta* group and, although described as a *Percrocuta*, it is now referred to *Adcrocuta* (i.e. *A. australis*). This is done because a close relative and possible ancestor, the Eurasian '*Percrocuta*' *eximia*, is now generally regarded as an *Adcrocuta* (Ficcarelli & Torre 1970; Schmidt-Kittler 1976). *A. australis* has some characters in common with the *Euryboas*, but is distinguished by its larger size, lower crowned and stouter canines, occasional presence of anterior accessory cusps on P_2 and P_3 , longer carnassials, and unicuspid M_1 talonid. The *A. australis* sample used in this study was derived from the Quartzose Sand

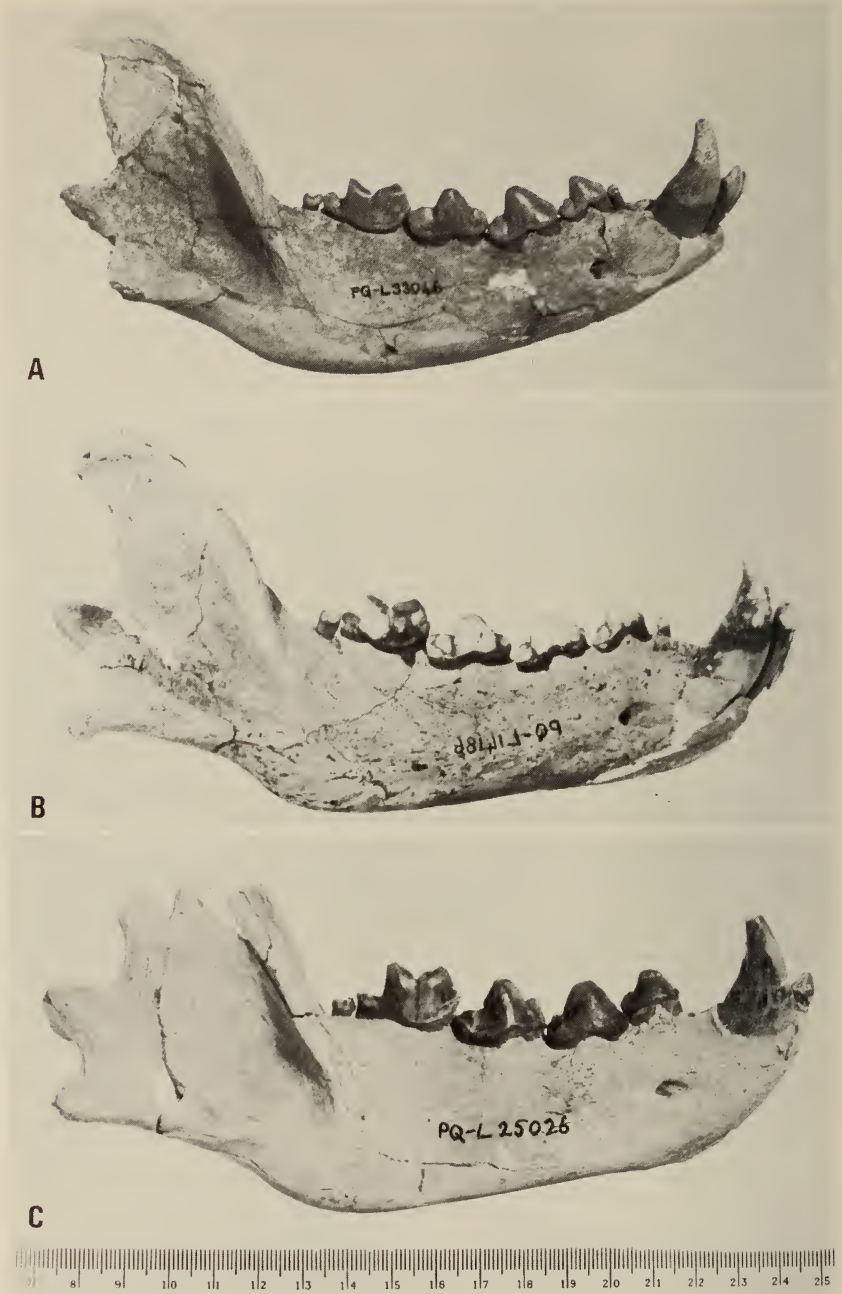


Fig. 1. Lateral views of hyaenid hemimandibles from Langebaanweg. A. *'Hyaenictis preforfex'* (L33046). B. *Hyaena abronia* (L14186) (reversed). C. *'Hyaena' namaquensis* (L25026).

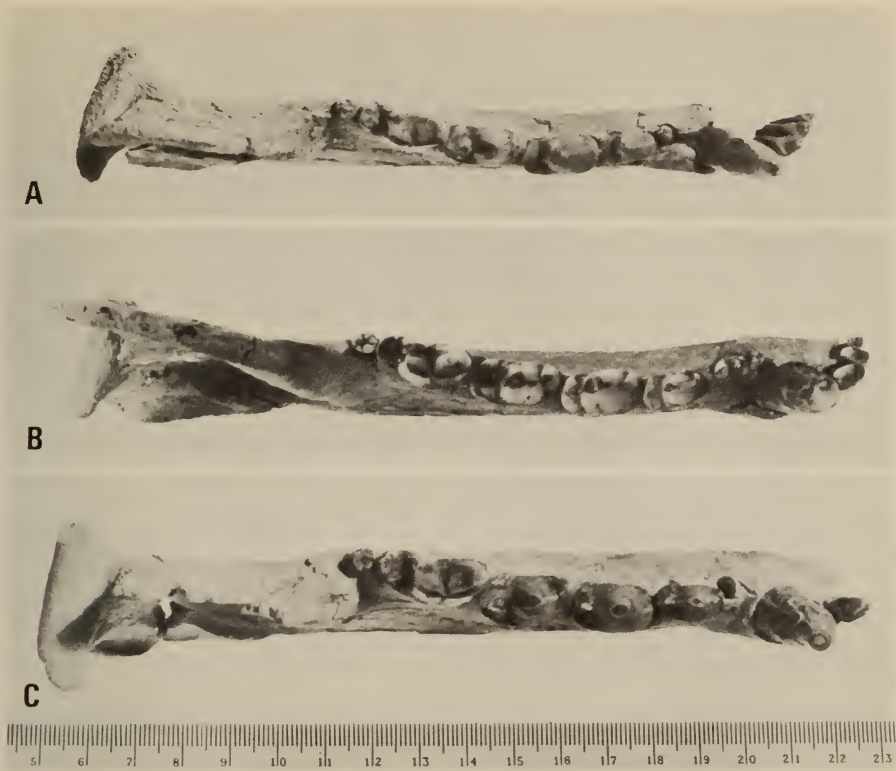


Fig. 2. Occlusal views of hyaenid hemimandibles from Langebaanweg. A. *'Hyaenictis' preforfex* (L33046). B. *Hyaena abronia* (L14186) (reversed). C. *'Hyaena' namaquensis* (L25026).

Member, but it is also known from the Pelletal Phosphorite Member and is apparently not confined to deposits of a particular type.

The 'E' Quarry hyaenids appear to be unique in providing evidence of a progression in an evolutionary sense from Eurasian late Miocene hyaenids, while at the same time maintaining the pattern of their representation. In other words, there is apparently no other Old World fauna of comparable age which includes a variety of hyaenid species which are reminiscent of the Eurasian late Miocene. In order to justify this observation recorded Eurasian late Miocene taxa are compared and contrasted with those from Langebaanweg.

THE HYAENA GROUP

Plioviverrops orbigny is the smallest of the Eurasian species and one which evidently does not have a counterpart at Langebaanweg. This species may have become extinct without issue, although Thenius (1966) suggested it as a possible ancestor of *Proteles cristatus*, a species whose fossil history is largely unknown except for a Pleistocene species from the Transvaal (Hendey 1974b).

The European *Ictitherium robustum* and Chinese *I. gaudryi* have long been recognized as closely related forms and they may be conspecific. The situation in respect of *Palhyaena hipparionum* and *P. wongii* is similar. By contrast, the Chinese *Hyaenictitherium hyaenoides* apparently had no European counterpart, but together with *Ictitherium* and *Palhyaena* is part of a close-knit combination within the *Hyaena* group which has been thoroughly examined by Kurtén (1954), amongst others.

Schmidt-Kittler (1976) cast some doubt on the status of *Hyaenictitherium*, claiming that it does not even merit separate subgeneric status. *H. hyaenoides* is nevertheless distinguishable from the classic *Palhyaena*, the taxon which Schmidt-Kittler regards as the stem form. The classification of taxa in such situations is prone to be controversial and Schmidt-Kittler's 'lumping' is justifiable. However, the evolution of this group of hyaenids is here interpreted as successive branching from a primary lineage, with each additional branch representing a new genus (Fig. 3).

This arrangement can be justified only if later, well differentiated representatives of individual branches are recognized. Thus the earliest member of a new lineage, although essentially similar to the stem form, is distinguished at the genus level if it can be established that it had descendants whose characteristics are clearly different from those of members of the stem lineage. Certain of the Langebaanweg hyaenids are relevant to the recognition here of *Ictitherium*, *Palhyaena* and *Hyaenictitherium* as distinct genera.

The '*Hyaenictis*' *preforfex*/*Hyaena abronia*/'*Hyaena*' *namaquensis* combination at Langebaanweg is reminiscent of the Eurasian trio referred to above. In

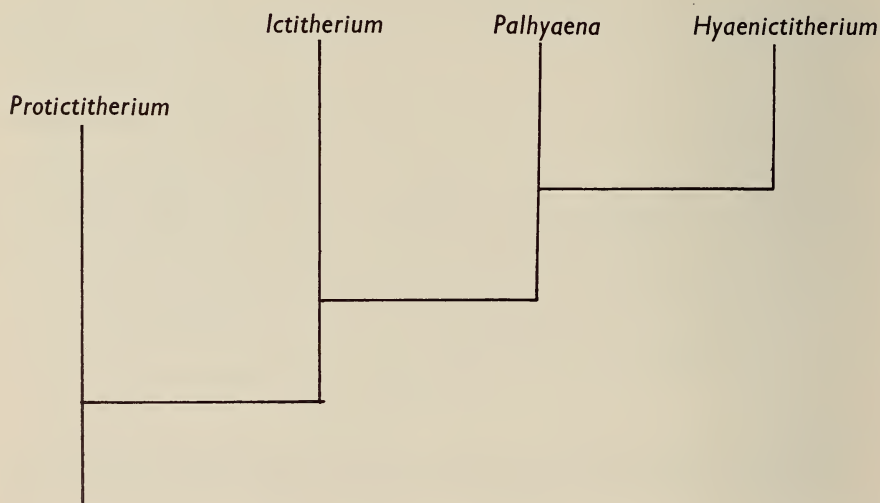


Fig. 3. Suggested phylogenetic relationships of some late Tertiary members of the *Hyaena* group.

each case size differences of no great magnitude are combined with differences in tooth proportions to distinguish associated species of the two combinations of taxa. In general, the Langebaanweg species are more advanced than those of the Eurasian late Miocene. For example, in the Langebaanweg species the molars (i.e. M^1 , M_1 talonid, M_2^2) are reduced relative to those of the Eurasian species. In addition, the species of the Langebaanweg series are larger than those of the Eurasian series, that is, '*H.*' *preforfex* is larger than *Ictitherium*, *H. abronia* is larger than *Palhyaena* and '*H.*' *namaquensis* is larger than *Hyaenictitherium*.

The simplest phylogenetic interpretation of the preceding observations would be to regard *Ictitherium* as the ancestor of '*H.*' *preforfex*, *Palhyaena* the ancestor of *H. abronia*, and *Hyaenictitherium* the ancestor of '*H.*' *namaquensis*, with the ancestral forms possibly being African counterparts of the recorded Eurasian species.

Having established this as a working hypothesis, the suggested interrelationships can be examined in more detail. Superficially there is nothing which would positively preclude the suggested relationships. Indeed they seem eminently feasible. For example, one of the more striking features of the two series of taxa is that in each case it is the smallest member which is the most primitive (i.e. viverrid-like).

In a study of the Eurasian taxa Kurtén (1954: 16–17, Fig. 9) used a ratio diagram of certain tooth lengths to illustrate similarities and differences. A similar ratio diagram for the Langebaanweg species is equally revealing (Fig. 4). Kurtén used *Palhyaena wongii* as a standard and in the case of the Langebaanweg series *Hyaena abronia* was selected since it is the suggested descendant of *Palhyaena*. It is worth noting that a ratio diagram using tooth breadths revealed an essentially similar pattern.

There are some remarkable similarities between the ratio diagrams of the Langebaanweg and Eurasian series. In their proportions the teeth of '*Hyaenictus preforfex*' and '*Hyaena*' *namaquensis* differ from the *Hyaena abronia* standard in much the same way as *Ictitherium robustum* and *Hyaenictitherium hyaenoides* differ from *Palhyaena wongii*. Interestingly, a much closer approach to the '*H.*' *preforfex* graph is achieved when the *I. robustum* and *I. gaudryi* samples are combined by drawing a new graph on Kurtén's Figure 9 equidistant from the graphs of the two *Ictitherium* species. This may not be a valid statistical procedure since the unpublished primary data for the two species should be combined in order to calculate accurate ratios for the combination. Nevertheless, the experiment must have produced a graph which is approximately correct.

The similarity between the ratio diagrams of the Langebaanweg and Eurasian samples strongly suggests that the three Langebaanweg species are interrelated in a manner which is comparable to the interrelationships between the Eurasian *Ictitherium*, *Palhyaena* and *Hyaenictitherium*. This is here interpreted as evidence in support of the ancestor/descendant relationships postulated earlier.

Not surprisingly the two ratio diagrams also differ in certain respects. For

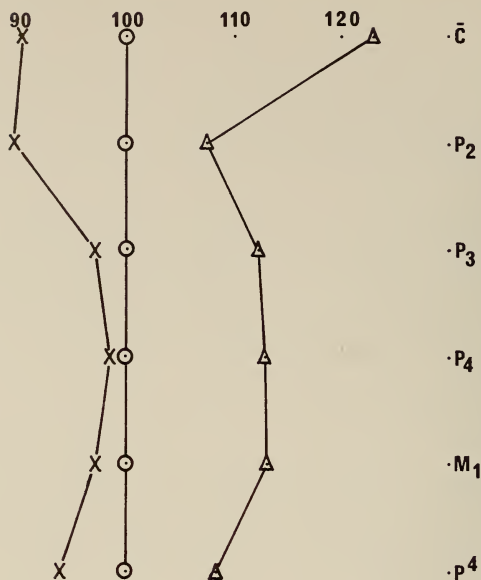


Fig. 4. Ratio diagram comparing mean lengths of lower teeth and P_4 in certain Langebaanweg Hyaenidae: '*Hyaenictis preforfex*' (X), '*Hyena namaquensis*' (Δ). Standard of comparison (100%): *Hyena abronia* (O).

example, in terms of its tooth proportions '*H. preforfex*' is closer to *H. abronia* than are either of the Eurasian *Ictitherium* species to *P. wongii*. This applies particularly in the case of the posterior premolars (P_3 , P_4). This is also illustrated by a second ratio diagram (Fig. 5), in which the lower cheektooth lengths of the Langebaanweg species are plotted against an *I. robustum* sample as standard.

Figure 5 illustrates even more clearly than Figure 4 that the tooth proportions of '*H. preforfex*' and '*H. namaquensis*' are essentially similar and that *H. abronia* differs from them principally in its premolar development. An increase in premolar size is one of the more general rules in hyaenid evolution and their marked size increase in '*H. preforfex*' and '*H. namaquensis*' relative to the condition in *I. robustum* is not surprising, since the latter species is a generalized form which presumably resembles the common ancestor of this group of hyaenids. Evidently the situation in respect of premolar development in *H. abronia* was somewhat different. A possible explanation for this situation emerges from an examination of the hypothetical lineage which includes *H. abronia*.

This lineage, which has *Ictitherium* as the stem form and with *Palhyaena*, *H. abronia* and the living *Hyaena hyaena* as subsequent members (Hendey 1974a, this report), may well prove to be less controversial than others suggested here.

There is little difference in overall body size and tooth characters in later members of the lineage, that is, *H. abronia* through to living *H. hyaena*. This suggests that the evolution of at least some characters had virtually ceased by the time an *H. abronia*-like stage had been reached. Since some recorded *Palhyaena* specimens seem to be little different from the Langebaanweg *H. abronia*, the lineage had evidently reached an 'optimum' stage relatively early. In other words, the 'Hyaena' condition was achieved precociously.

Evidently the same did not apply to the *Ictitherium*-'*H.*' *preforlex* and *Hyaenictitherium*-'*H.*' *namaquensis* lineages, where development of characters such as premolar size continued. They were thus slower in reaching an 'optimum' condition.

Another important point which is clearly illustrated by the accompanying ratio diagrams concerns the development of the canines. Kurtén (1954: 16) found *Hyaenictitherium hyaenoides* to be 'fairly similar' in tooth proportions to *Palhyaena* 'with the exception of the powerful canines'. This is also the character which most readily distinguishes the Langebaanweg '*H.*' *namaquensis* from its two contemporary near relatives. The implication is that *H. hyaenoides* and '*H.*' *namaquensis* had the development of large canines as a character in common and, consequently, that they were, indeed, closely related.

There is, however, a complication with this interpretation of the data. Judging from Figure 5, canine size in the Langebaanweg species is approximately proportional to the overall size of the species concerned, something which is also evident, although perhaps less obvious, in Kurtén's (1954) ratio

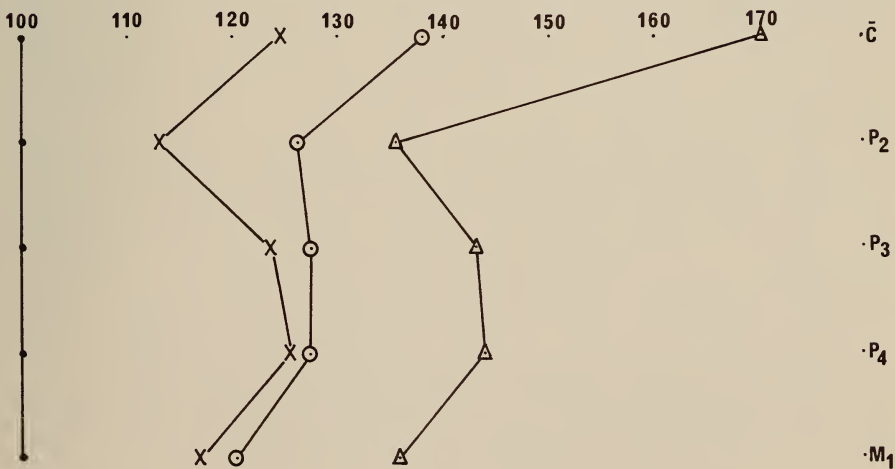


Fig. 5. Ratio diagram comparing mean lengths of lower teeth in certain Langebaanweg Hyaenidae: '*Hyaenictis*' *preforlex* (X), *Hyaena abronia* (O), '*Hyaena*' *namaquensis* (Δ). Standard of comparison (100%): European *Ictitherium robustum* (Kurtén 1954).

diagram. It is therefore possible that the large canine size in *H. hyaenoides* and '*H.*' *namaquensis* is due not to a phylogenetic connection, but simply to the fact that they are the largest members of their respective series. This means that canine size, and indeed the overall similarities in tooth proportions in the two series, may be coincidental.

Coincidence can, of course, not be ruled out, but it must be highly improbable. Not only do the two series have similar patterns in tooth proportions which go together with evolutionary advances in tooth morphology (e.g. reduced molar size in the Langebaanweg series), but in the case of the *Palhyaena*–*H. abronia* lineage at least, there is evidence of advances in the postcranial skeleton as well (Hendey 1974a: 116, table 20). Furthermore, if the Langebaanweg series did not evolve from the suggested late Miocene taxa, alternatives must be sought and certainly none are obvious.

Whereas the evolution of *H. hyaena* from the *Palhyaena*–*H. abronia* combination appears likely, the subsequent histories of the *Ictitherium*–'*H.*' *preferfex* and *Hyaenictitherium*–'*H.*' *namaquensis* lineages are obscure. The former almost certainly has no living descendant, but the latter could be ancestral to *Hyaena brunnea*.

The first fully mature '*H.*' *namaquensis* specimen from Langebaanweg (SAM-PQ-L25026) is similar in overall size to living *H. brunnea*. The fossil species differs in some body proportions such as, for example, having longer hind limbs. This difference is similar to one which distinguishes *H. abronia* from *H. hyaena* (Hendey 1974a: 116–118). There are also some marked differences in the dentitions of '*H.*' *namaquensis* and *H. brunnea*. For example, the former retains P_1 and M_2^2 and has lower crowned and more slender premolars. These, and other differences, all indicate the primitive state of '*H.*' *namaquensis* and all are likely to have been present in an early ancestor of *H. brunnea*. Consequently, there is apparently nothing to preclude an ancestor/descendant relationship between these taxa.

The situation is reminiscent of that which exists between *H. abronia* and *H. hyaena*, although in this instance the differences are less marked and there is an appropriate late Pliocene/early Pleistocene intermediate form recorded (i.e. *H. hyaena makapani*). It was suggested above that the hypothetical *Hyaenictitherium*–'*H.*' *namaquensis* lineage had apparently not reached an 'optimum' evolutionary state by the early Pliocene. If evolutionary advances continued during this epoch, they may well have been in the direction of an *H. brunnea*-like species. This would account for the fact that *H. brunnea* is the more specialized (advanced) of the two living *Hyaena* species. While a direct relationship between '*H.*' *namaquensis* and *H. brunnea* is here suggested as a possibility, more evidence is needed to test the hypothesis.

Whereas *Ictitherium*, *Palhyaena* and *Hyaenictitherium* form a close-knit unit within the late Miocene *Hyaena* group of Eurasia, the group apparently has at least two additional members, namely, *Hyaenictis* and *Lycyaena*.

For a reason given earlier, the Langebaanweg '*Hyaenictis*' *preferfex* is no

longer regarded as a member of that genus. There is, however, another of the Langebaanweg species which may be related to *Hyaenictis* or *Lycyaena*. This is the undescribed species of *Euryboas*.

The late Miocene ancestor of the Langebaanweg *Euryboas* is likely to have had the following amongst its characteristics:

1. M^2 reduced or absent.
2. M_1 metaconid present, although possibly smaller than in *Ictitherium*, *Palhyaena* and *Hyaenictitherium*;
3. M_1 talonid bicuspid;
4. M_2 persistently present, but P_1 absent or sometimes absent;
5. Postcranial skeleton similar in overall size to larger members of the *Ictitherium*/*Palhyaena*/*Hyaenictitherium* subgroup.

The last character is important in suggesting that *Euryboas* belongs to the *Hyaena* group rather than the *Percrocuta* group, since the late Miocene percrocucas were evidently relatively large, heavily-built animals. The other characters combine to suggest that *Euryboas* was derived from *Hyaenictis* or *Lycyaena*, rather than the *Ictitherium*/*Palhyaena*/*Hyaenictitherium* subgroup. Both *Lycyaena* (De Beaumont 1967) and *Hyaenictis* (Thenius 1966) have previously been suggested as possible *Euryboas* ancestors.

In the case of *Hyaenictis*, *H. graeca* is the species of appropriate age to be ancestral to a primitive *Euryboas*. This species apparently fulfils most of the required criteria for this role, but it does lack the M_1 metaconid. This is not necessarily a serious objection since this cusp is sometimes variably developed in hyaenid species (Kurtén 1956: 12–14), and the M_1 of *H. graeca*, like that of the Langebaanweg *Euryboas*, may sometimes have had a small metaconid. Alternatively, this cusp may have been present in an as yet unknown African counterpart of *H. graeca*.

The Eurasian late Miocene representative of *Lycyaena* is *L. chaeretis*, for which a similar complication exists. According to Pilgrim (1932) this species lacks M_2 , a tooth which is sometimes present in the Langebaanweg *Euryboas*. Zapfe (1948) has, however, recorded a *L. chaeretis* from Austria in which a small M_2 was present. The presence of M_2 may have characterized certain late Miocene populations of *Lycyaena*, including an African one, if it existed.

On balance the other recorded characteristics of *Lycyaena* appear to be more *Euryboas*-like than those of *Hyaenictis* and the former is here regarded as the likely ancestor of *Euryboas*.

Later species of *Euryboas* are recorded from elsewhere in Africa and in Europe. Some of the specimens previously included in this genus were recently referred instead to *Chasmaporthetes* (Galiano & Frailey 1977).

THE PERCROCUTA GROUP

The last of the 'E' Quarry hyaenids, *Adcrocuta australis*, was once thought to be the least problematical of the species, since its large size and certain specialized dental characters readily distinguished it from its contemporaries.

The increase in the sample size has revealed that there is appreciable variation in this species, which may be due at least in part to sexual dimorphism, and some cranial material apparently belonging to *A. australis* resembles specimens assigned to *Euryboas*.

Even when allowance is made for marked sexual dimorphism, and problematical fragmentary specimens are excluded from consideration, the material assigned to *A. australis* is more variable than that belonging to other Langebaanweg hyaenids. Indeed, there are grounds for suspecting that the material may belong to two species. An essentially similar situation was encountered by Zdansky (1924) when he studied the Chinese *A. eximia variabilis*. His decision to recognize only one variable species has been generally supported (e.g. Pilgrim 1931; Kurtén 1957). With this precedent in mind, and since *A. eximia* is regarded as the structural ancestor of *A. australis* (Hendey 1974a), the material assigned to the latter is left undivided.

The Langebaanweg *A. australis* and *Euryboas* have certain dental characters in common. For example, their cheekteeth are generally similar in morphology (Fig. 6) and in proportions (Fig. 7). These two species are readily distinguished from the other Langebaanweg hyaenids, and this raises the possibility that the *Euryboas* belongs in the *Percrocuta*, rather than *Hyaena* group. Although this possibility cannot be dismissed, it is not favoured since *A. australis* does have some specialized characters not evident in *Euryboas*, which suggests that the two species belong to lineages which had had a long, separate history. For example, *A. australis* was a large animal with robustly proportioned postcranial bones, whereas the *Euryboas* was smaller and more lightly built. *A. australis* is also distinguished by specialized dental characters such as sometimes having prominent anterior accessory cusps on P_2 and P_3 and in having a unicuspid M_1 talonid.

The similarities between *A. australis* and the *Euryboas*, which are here ascribed to parallel evolution, will be discussed again in a later section of this report.

NOMENCLATURE

Having reviewed the status and relationships of the 'E' Quarry hyaenids, the taxonomic implications of the conclusions reached here can be considered.

Since '*Hyaenictis*' *preforlex* is regarded as a descendant of late Miocene *Ictitherium*, and since the subsequent history of the lineage is not known, the Langebaanweg species is referred to *Ictitherium* on the principle that members of a single lineage are congeneric.

The situation in respect of *Hyaena abronia* remains unchanged, although a new complication now arises. In this instance both ancestral (*Palhyaena*) and descendant (*H. hyaena*) forms are recognized and, in order to conform to the principle stated above, *Palhyaena* should be sunk into *Hyaena*, the latter being the name which has priority. This step is, however, not formally proposed since there is no point in synonymizing a name in common use if the reason for doing



Fig. 6. Lateral and occlusal views of hyaenid hemimandibles from Langebaanweg. A. *Euryboas* sp. (L21000) (immature adult). B. *Adcrocuta australis* (L22204).

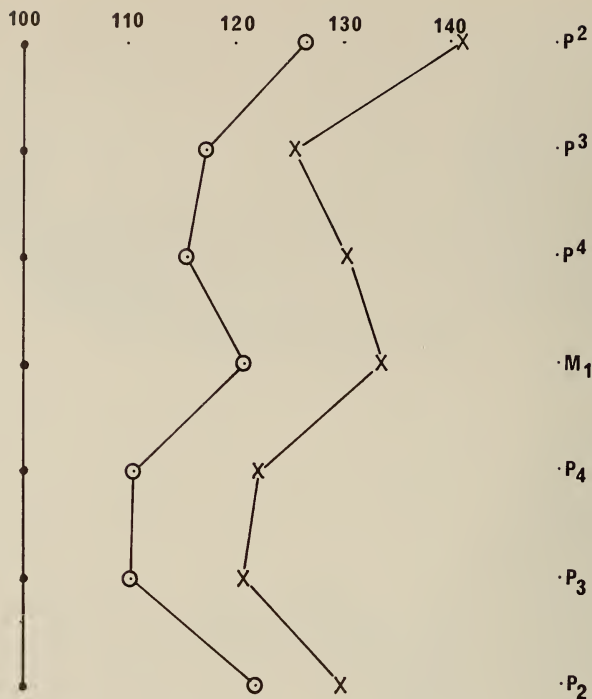


Fig. 7. Ratio diagram comparing mean lengths of upper and lower teeth of Langebaanweg *Euryboas* sp. (O) and *Adcrocuta australis* (X). Standard of comparison (100%): *Hyaena hyaena*.

so is not generally accepted. A decision can await reactions to the suggestion.

'*Hyaena*' *namaquensis*, like *Ictitherium preforfex*, is referred to its supposed ancestral genus, in this instance, *Hyaenictitherium*. The name becomes *Hyaenictitherium namaquense*. If substantiated, the suggestion that *H. namaquense* is ancestral to *Hyaena brunnea* will provide a solution to the problem of the generic name of the latter. At least twice in recent years it has been indicated that the relationship between *H. hyaena* and *H. brunnea* is distant enough to warrant nomenclatural distinction above the species level (Hendey 1974a: 148-149; Galiano & Frailey 1977: 11-12). *Hyaenictitherium* probably has priority over any other generic name available for '*Hyaena*' *brunnea*.

In spite of the problems and doubts about relationships mentioned earlier, no name changes are proposed in the cases of *Adcrocuta australis* and the unnamed *Euryboas* species.

The Langebaanweg ('E' Quarry) hyaenids now recognized are listed in Table 1. The suggested relationships of the taxa already discussed are summarized in Figure 8. In all instances the ancestral forms are merely recorded

species in an appropriate evolutionary state for this role and they need not have been in the actual ancestral position. For example, the Chinese *Hyaenictitherium hyaenoides* was almost certainly not a direct ancestor, but was simply a structural ancestor of the South African *H. namaquense*. It is much more likely that the latter stemmed from an as yet unknown African late Miocene *Hyaenictitherium* which resembled *H. hyaenoides*, but which was not necessarily conspecific with it.

The tooth sizes of the samples used in this study are recorded in Table 2.

RELATIONSHIPS OF *CHASMAPORTHETES*

In a recent note on the origins of North American *Chasmaporthetes*, the Chinese late Miocene *Aderocuta eximia variabilis* was suggested as a likely ancestor (Hendey 1975). In recording what they regard as the first Asiatic *Chasmaporthetes* (*C. kani*), Galiano & Frailey (1977: 9) concluded that this genus 'was apparently generically distinct before its entry into North America and shares a number of derived characters with *Euryboas* rather than with *Percrocuta*'. This conclusion was based on a cladistic analysis of the Hyaenidae other than the percrocutas.

The omission of the percrocutas was justified on the grounds that they retain 'a number of primitive characters' in association with others that are 'highly derived', which sets them apart from other hyaenids, including *Chasmaporthetes* (Galiano & Frailey 1977: 9). The derived characters mentioned are a reduced P⁴ protocone and contact between the premaxillary and frontal

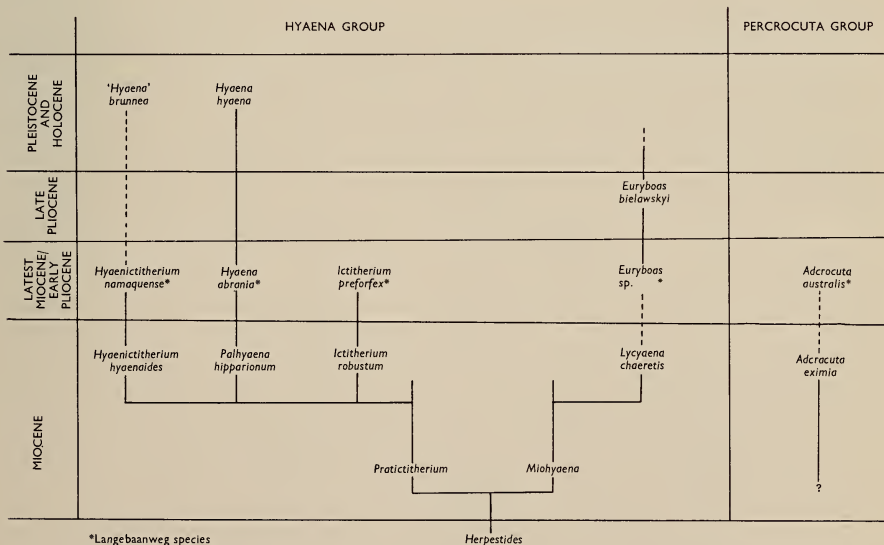


Fig. 8. Tentative phylogeny of some Hyaenidae.

TABLE 2
Mean dimensions of Langebaanweg Hyaenidae teeth.

	\bar{C}		P ¹		P ²		P ³		P ⁴		M ¹		M ²	
	l	b	l	b	l	b	l	b	l	b	l	b	l	b
<i>Ictitherium preforfex</i> (n = 7)	12,1	9,1	5,6	4,7	13,8	7,7	18,7	11,4	26,3	15,3	7,9	13,1	3,6	5,3
<i>Hyaena abronia</i> (n = 4)	11,9	9,8	6,2	5,1	14,4	8,2	18,9	11,4	28,0	15,7	9,3	15,0	4,0	5,3
<i>Hyaenictitherium namaquense</i> (n = 3)	15,3	11,4	7,9	6,7	16,4	9,2	21,4	13,6	30,3	17,8	9,3	16,5	—	—
<i>Euryboas</i> sp. (n = 2)	15,7	11,8	7,0	7,3	20,0	11,5	23,9	14,5	34,7	19,5	7,8	15,8	0	0
<i>Adcrocuta australis</i> (n = 8)	16,8	12,6	8,1	8,7	22,3	12,2	25,6	16,1	39,2	20,2	—	—	?	?
	\bar{C}		P ₁		P ₂		P ₃		P ₄		M ₁		M ₂	
	l	b	l	b	l	b	l	b	l	b	l	b	l	b
<i>Ictitherium preforfex</i> (n = 7)	12,1	9,2	3,2	3,4	12,1	7,3	16,7	9,6	18,3	9,6	20,2	9,3	4,5	4,2
<i>Hyaena abronia</i> (n = 4)	13,4	10,2	4,1	3,7	13,5	7,6	17,2	9,6	18,6	9,8	20,8	10,3	5,2	4,5
<i>Hyaenictitherium namaquense</i> (n = 3)	16,5	11,7	3,8	4,6	14,5	8,3	19,3	10,9	21,0	11,2	23,5	10,7	5,6	5,2
<i>Euryboas</i> sp. (n = 2)	15,5	11,4	0	0	16,9	9,1	20,9	11,2	22,8	11,7	25,2	12,0	—	—
<i>Adcrocuta australis</i> (n = 8)	17,6	12,8	0	0	18,0	9,9	22,9	12,3	25,0	12,7	27,9	12,7	—	—

bones of the skull, while the only primitive character mentioned was the presence of a large metacarpal I. While the omission of most percrocutas on these grounds may be justified, this does not apply in the case of *A. eximia variabilis*.

A large metacarpal I, which amongst living taxa is found only in *Proteles*, undoubtedly is a 'primitive' character, but it was a feature of most, if not all, late Tertiary hyaenids. This certainly applies in the case of all five species recorded from 'E' Quarry.

Although the P⁴ protocone generally is reduced in the percrocutas (Kurtén 1957), *A. eximia variabilis* is exceptional in having this cusp of variable size (Zdansky 1924: 96; Pilgrim 1931: 117; Kurtén 1957: 399). Evidently in the case of certain individuals at least, the P⁴ protocone was not necessarily any smaller than that in *C. kani*, in which this cusp is also somewhat reduced (Galiano & Frailey 1977: fig. 1).

The contact between the premaxillaries and frontals is not a constant character in *A. eximia variabilis*, Zdansky (1924) having recorded one specimen in the series he studied in which there was no such contact. This character is also variable in some other hyaenids. For example, a series of 13 *Crocuta crocuta* skulls in the South African Museum includes 7 specimens in which there is no contact between these bones, 1 specimen in which there is contact on one side only, and 5 specimens in which there is contact. Galiano & Frailey were thus mistaken both in regarding the maxillary-frontal contact in *A. eximia variabilis* as constant, and in regarding it as unique.

Since there are now no recorded grounds for dismissing the possible phylogenetic link between *A. eximia variabilis* and *Chasmaporthetes*, it is here examined in some detail.

North American *Chasmaporthetes* undoubtedly had an Asian ancestor, and Galiano & Frailey (1977) have provided evidence that the Chinese *C. kani* is an appropriate candidate for this role, at least in terms of morphology. Consequently the theory that *Chasmaporthetes* and *Adcrocuta* are closely related can most conveniently be tested by comparing *C. kani* with the Chinese *A. eximia variabilis* described by Zdansky (1924). The comparison is facilitated by the fact that both species are represented by fairly complete and well-preserved specimens belonging to several individuals.

In the comparisons which follow account is also taken of the undescribed *Euryboas* from Langebaanweg. It is relevant because if Galiano & Frailey are correct in concluding that *Chasmaporthetes* and *Euryboas* were closely related, then the Langebaanweg species should, because of its age relative to recorded *Chasmaporthetes*, be a more appropriate structural ancestor of the latter than is *A. eximia variabilis*. Mention will also be made of the Langebaanweg *A. australis* since it is evidently intermediate in age between *A. eximia variabilis* and *C. kani*, and, if the latter two taxa are phylogenetically related, *A. australis* should also have characters in common with *C. kani*.

The skulls and mandibles of *C. kani* and *A. eximia variabilis* are superficially similar morphologically and little different in size. The mandible of *Euryboas*

may, on average, be more slender than those of the other two taxa, but this possible difference has yet to be substantiated. There is certainly a greater similarity between the mandible of *C. kani* and certain of the Langebaanweg *A. australis* specimens than between that of the former and the Langebaanweg *Euryboas*.

One of the more striking characteristics of the mandible in *Euryboas* is that the corpora are remarkably straight, the two halves being steadily divergent from the symphysis. Viewed ventrally the mandible is V-shaped. In this respect *Euryboas* resembles all other members of the *Hyaena* group, living and fossil, examined during the course of the present study. By contrast, at least some of the mandibles of *A. australis*, *A. eximia* (e.g. Schmidt-Kittler 1976: pl. 3, fig. 6) and North American *Chasmaporthetes* (e.g. Stirton & Christian 1940: fig. 1) have markedly curved corpora and, viewed ventrally, are almost U-shaped. This also applies to some specimens in the available series of living *C. crocuta* specimens, in which four out of seven specimens have curved jaws.

Since mandibular curvature is not constant in any one species, it is an unreliable distinguishing character. However, it may be significant that curved mandibles were observed only in species which are, or which might be, members of the *Percrocuta* group. *Adcrocuta* and *Chasmaporthetes* are here regarded as *percrocucas*, while *C. crocuta* may be, even though it is generally included in the *Hyaena* group (e.g. Thenius 1966; Galiano & Frailey 1977). This may be an instance where a character (i.e. curved mandibles) is indicative of one group only (i.e. the *percrocucas*), whereas the opposite condition (i.e. straight mandibles) is found in both groups of hyaenas. Further observations are required to test this hypothesis.

Jaw shape is usually an indication of the shape of the cheektooth rows, although there are instances where straight jaws (viewed ventrally) occur together with curved cheektooth rows. This applies in the case of, for example, '*Hyaena*' *brunnea*. Toothrow curvature has, therefore, to be considered as a separate character.

Galiano & Frailey (1977) have pointed out that in *Euryboas* the cheektooth rows are straight, whereas in *Chasmaporthetes* they are curved. The latter condition is evident in both *A. eximia variabilis* and *A. australis*, even when the jaws are straight. The primitive Langebaanweg *Euryboas*, like later forms, has straight cheektooth rows, which is an indication that this was a characteristic of the lineage for most, and probably all, of its history. The implication is that *Euryboas* and *Chasmaporthetes* had evolved independently at least since late in the Miocene.

As with the mandibles, there is a greater similarity between the teeth of *C. kani* and *A. australis* than between those of the former and *Euryboas*. In addition, there is a general similarity between the teeth of these three taxa and those of *A. eximia variabilis*, although it is on the differences which do exist that the question of interrelationships hinges.

Ratio diagrams are used to illustrate some of the similarities and differences

in tooth proportions in *A. eximia variabilis*, *C. kani* and the Langebaanweg *Euryboas* (Fig. 9). There is a basic similarity in the patterns of tooth length in the three taxa. The premolars of *C. kani* are only slightly shorter than those of *A. eximia variabilis*, whereas the carnassials are appreciably shorter (Fig. 9A). By contrast, the carnassials of *C. kani* and the *Euryboas* are of comparable length, whereas the anterior premolars of the latter are longer (Fig. 9B). Thus if the *Euryboas* represents the structural ancestor of *C. kani*, then the evolutionary trend in respect of cheektooth length was reduction of premolar length. Alternatively, if *A. eximia variabilis* was the ancestor, then the trend was reduction of carnassial length.

One of the metrical characters not illustrated in the accompanying ratio diagrams is crown height of the canines. The canines of *A. eximia* and North American *Chasmaporthetes johnstoni*, and possibly also *C. kani*, are unremarkable, relatively low-crowned teeth, whereas the canines of the Langebaanweg *Euryboas* are relatively high-crowned. The length: crown height ratio for the C of specimen SAM-PQ-L21000 is 1 : 2, which compares closely to the ratio

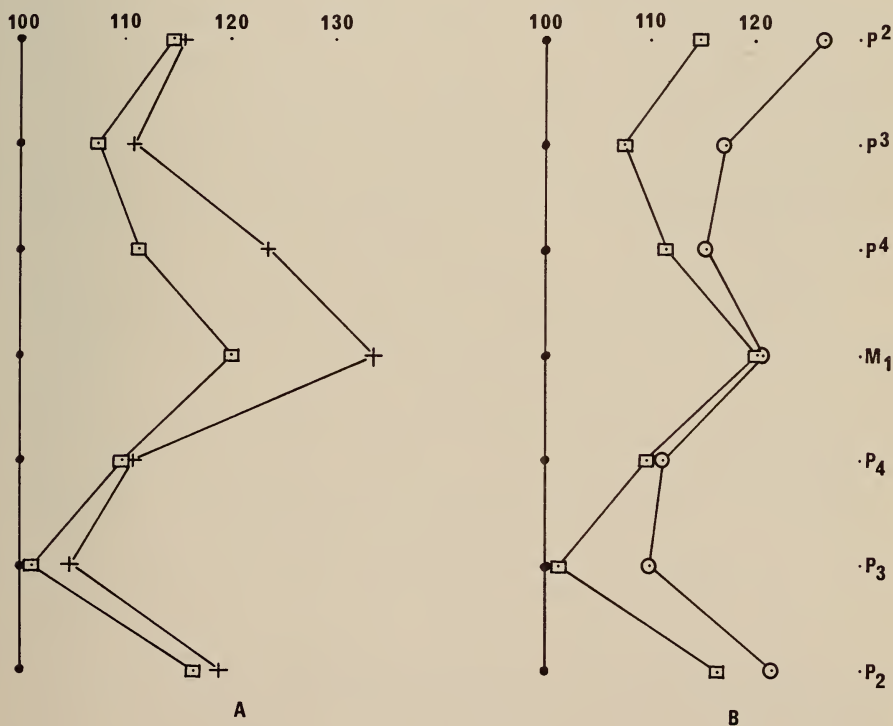


Fig. 9. Ratio diagrams comparing mean lengths of upper and lower teeth of *Aderocuta eximia variabilis* (+) (Kurtén 1957), *Chasmaporthetes kani* (□) (Galiano & Frailey 1977), and the Langebaanweg *Euryboas* sp. (○). Standard of comparison (100%): *Hyaena hyaena*.

of 1 : 1,97 in the *E. bielawskyi* from Roccaneyra (Schaub 1941). The ratio in *C. johnstoni* is 1 : 1,79, while in one of the Langebaanweg *A. australis* specimens (L22204) it is 1 : 1,63. The canine height in *Euryboas* is clearly a specialized character, which is not shared by at least some, and perhaps all, species of *Adcrocuta* and *Chasmaporthetes*. Thus in terms of canine development *Adcrocuta* is more appropriate than *Euryboas* as an ancestor for *Chasmaporthetes*.

C. kani differs from *A. eximia variabilis* in having a slightly larger P¹. Galiano & Frailey (1977: 6) are of the opinion that the P¹ of *C. kani* 'is proportionally larger than in any other hyaenid genus'. No explanation of this character is offered but, since it is apparently unique, it must be regarded as a specialization. By curious contrast in view of their conclusion on relationships, Galiano & Frailey record the absence of P¹ as one of the characteristics of *Euryboas*. In fact, this tooth is present in the primitive Langebaanweg species. Since this species was ancestral to forms which had lost P¹, it is perhaps unlikely that it should also be the ancestor of another (i.e. *C. kani*) in which this tooth was unusually well developed. No such anomaly exists in respect of *Adcrocuta*, which would, therefore, be a more appropriate ancestral form for *C. kani*.

C. kani also differs from *A. eximia variabilis* in lacking P₁, a tooth which is usually present in the latter. The reduction and eventual loss of P₁ is a general rule in hyaenid evolution, so in respect of this tooth *C. kani* could well have evolved from *A. eximia variabilis*, a species in which loss of P₁ was already being manifested. On the other hand, the Langebaanweg *Euryboas* would be an equally appropriate structural ancestor since, like *C. kani*, it lacks P₁.

The P₂², P₃³ and P₄ of *C. kani* and *A. eximia variabilis* are of comparable length, but those of *C. kani* are narrower (Table 3), the latter being a difference

TABLE 3

Mean dimensions of *Chasmaporthetes kani* and *Adcrocuta eximia variabilis* teeth.

	P ¹		P ²		P ³		P ⁴		M ¹	
	l	b	l	b	l	b	l	b	l	b
<i>Chasmaporthetes kani</i> ¹	8,8	7,8	18,1	11,3	21,9	13,7	32,6	18,0	7,6	16,4
<i>Adcrocuta eximia variabilis</i> ²	7,1	7,4	18,1	12,5	22,6	16,0	38,4	19,0	6,1	13,6

	P ₁		P ₂		P ₃		P ₄		M ₁	
	l	b	l	b	l	b	l	b	l	b
<i>Chasmaporthetes kani</i> ¹	0	0	15,8	9,0	19,2	10,7	22,3	11,8	25,1	11,4
<i>Adcrocuta eximia variabilis</i> ²	5,3	5,9	16,4	11,8	19,7	14,2	22,2	13,8	27,5	13,1

¹ Galiano & Frailey 1977.

² Zdansky 1924.

not shown on the ratio diagram (Fig. 9A). The Langebaanweg *Euryboas* has premolars comparable in breadth to those of *C. kani* but which are, with the exception of P_4 , slightly longer. Advanced *Chasmaporthetes*, like *Euryboas*, has narrow, sectorial premolars as a major distinguishing characteristic. It follows that while derivation of *C. kani* from *A. eximia variabilis* would be logical in terms of the relative development of their premolars, derivation of the former from the Langebaanweg *Euryboas* is not, since even this primitive *Euryboas* was already more specialized in terms of premolar proportions.

Also relevant here is the observation by Galiano & Frailey (1977: 2) that the 'anterior accessory cusps of P_2 and P_3 [in *C. kani* are] relatively weak as compared with other *Chasmaporthetes* species'. In this respect *C. kani* occupies a position intermediate between *A. eximia variabilis* and advanced *Chasmaporthetes*, an appropriate position in the hypothetical *Adcrocuta*-North American *Chasmaporthetes* lineage. Assuming that Galiano & Frailey were correct in reassigning some Old World hyaenids to *Chasmaporthetes*, then it appears that *Euryboas* never did develop prominent anterior accessory cusps on the anterior premolars. This need not necessarily exclude the Langebaanweg *Euryboas* from the role as structural ancestor of *Chasmaporthetes* but, as in the case of P^1 , it would be another instance where descendant forms evolved different characteristics.

The shapes of the anterior lower premolars are also significant. In *Chasmaporthetes* these teeth tend to be ovate in occlusal view, whereas in *Euryboas* they are more or less rectangular in outline. This is most obvious in the case of P_3 . In *A. eximia variabilis* and *A. australis* the P_3 's are rectangular, and in this respect they resemble most, if not all, contemporary hyaenids. Rectangularity in the lower premolars is thus a primitive condition, and their ovate shape in *Chasmaporthetes*, combined with the narrowness of these teeth, appears to be unique amongst hyaenids.

The carnassials of *C. kani* differ from those of *A. eximia variabilis* by being shorter and, in the case of M_1 , in having a simple unicuspid talonid. The M_1 talonid in *A. eximia variabilis* is variably developed, but both entoconid and hypoconid may be prominent. The fact that the talonid is variable in this taxon suggests that it was already evolving away from the more complex condition characteristic of primitive hyaenids and tending towards that evident in *C. kani*. The significance of carnassial shortening in the hypothetical *A. eximia variabilis*-*C. kani* lineage is not known. Possibly the development of the premolars as more effective shearing teeth in *C. kani* reduced the demand on the carnassials for this function.

Galiano & Frailey (1977) record the absence of the metaconid and presence of a unicuspid talonid on M_1 as characteristics of *Euryboas*. This does not apply in the case of the primitive Langebaanweg species, which has a bicuspid talonid and sometimes has a metaconid. These features would not, however, exclude this species as a structural ancestor of *C. kani*.

Relevant here is the nature of the M_1 in the Langebaanweg *A. australis*.

Although this species, like *A. eximia variabilis*, exhibits appreciable variation in certain characters, its M_1 typically lacks the metaconid and has a unicuspid talonid. Thus *A. australis* and *C. kani* are similar in terms of M_1 morphology, whereas the Langebaanweg *Euryboas* is, in this respect, more primitive in an evolutionary sense. These comments also apply with respect to the anterior accessory cusps of the anterior lower premolars. This is here interpreted as a further indication that the relationships of *Chasmaporthetes* lie with *Adcrocuta* rather than with *Euryboas*.

The M^1 of *C. kani*, like the P^1 , is a little larger than that of *A. eximia variabilis*. As a general rule, hyaenid evolution is characterized by a reduction in the size of upper molars. Consequently, the increase in the size of the *C. kani* M^1 relative to that of its hypothetical *A. eximia variabilis* ancestor is an anomaly which requires explanation. A similar situation exists in the case of the *Euryboas* lineage and it will be discussed first.

The M^1 of the Langebaanweg *Euryboas* is relatively large and more transversely elongated compared with those of other members of the *Hyaena* group from Langebaanweg. The transverse elongation is emphasized by the reduction of the metastyle and the root which supports it. Judging from a cast of the Val d'Arno *E. bielawskyi* maxillary fragment described by Schaub (1941), the M^1 of this species was even more transversely elongated, while the metastyle and supporting root were apparently absent. Indications are that the transverse elongation of M^1 was a progressive character in the *Euryboas* lineage and must, therefore, have been of functional advantage in the otherwise essentially sectorial dentition of this genus.

In primitive or unspecialized hyaenids, of which the living *Hyaena hyaena* is an example, the M^1 occludes with the posterior parts of M_1 , food being crushed between the occlusal surfaces of the M^1 and the M_1 talonid. In specialized species such as *Crocuta crocuta* the shearing blades of the carnassials are highly developed, the M_1 talonid is small and the M^1 reduced or absent. *Euryboas* is clearly quite different from either of the above examples since the M^1 appears disproportionately large in relation to the size of the M_1 talonid.

The M^1 in carnivores is not necessarily used only for crushing food. Even in such groups as the Felidae, in which the cheekteeth are highly sectorial and the M_1 talonid is absent in all but primitive forms, an M^1 is present. In such cases the M^1 also has a shearing function. As the jaws are closed the apex of the M_1 protoconid passes across the P^4 metastyle in a manner normal for carnivore carnassial shear. Thereafter it comes into contact with the anterior edge of M^1 and the posterior keel of the protoconid slides along this edge with a slicing action, which is at right angles to the main carnassial shear. Presumably it is occlusion of this kind which had developed to a high degree in *Euryboas*. In this instance there was the added refinement provided by the M_1 talonid, itself sectorial in advanced species, which slid across the occlusal surface of the M^1 , probably with a cutting, rather than crushing, action.

The Langebaanweg *Euryboas* was relatively primitive in having a bicuspid

M₁ talonid and, in addition, it sometimes had a small M₂. Thus, in this species the crushing function of the molars had not yet been completely replaced by the shearing function evident in later *Euryboas*.

The situation in the hypothetical *Adcrocuta*-*Chasmaporthetes* lineage was probably essentially similar and the relatively large M¹ of *C. kani* may be interpreted as a specialized, rather than primitive, character.

The M¹ of the Langebaanweg *Euryboas* is comparable in size to that of *C. kani* and this may be yet another indication that there was no direct phylogenetic link between them. There evidently was transverse elongation (i.e. size increase) in M¹ on the Langebaanweg *Euryboas*-*E. bielawskyi* lineage, but nothing comparable in the case of *C. kani* if it, too, stemmed from a *Euryboas* resembling that from Langebaanweg. This would be yet another example of possible descendants of the Langebaanweg *Euryboas* following different evolutionary trends. While this is, of course, not impossible, it is unlikely.

The postcranial skeleton of *Chasmaporthetes* has yet to be recorded but, since the dentition of this genus deviates markedly from those of most hyaenids and in some respects resembles that of *Euryboas*, it is possible, and perhaps even likely, that the postcranial skeleton also differed from those of 'conventional' hyaenids, and that it shared the specializations evident in *Euryboas*.

To sum up, the observable similarities and differences between the taxa discussed here combine to weight the evidence in favour of an *Adcrocuta* rather than *Euryboas* origin for *Chasmaporthetes*. All those characters in which the dentition of early Pleistocene *C. kani* differs from that of late Miocene *A. eximia variabilis* may be interpreted as advanced and none would exclude the latter from an ancestral role. Most of the differences reflect stages in the development of the highly sectorial postcanine dentition characteristic of North American *Chasmaporthetes*, and *C. kani* is, in an evolutionary sense, in an intermediate position in the hypothetical *A. eximia variabilis*-North American *Chasmaporthetes* lineage suggested earlier (Hendey 1975). The similarities between *A. eximia variabilis*, *C. kani*, and North American *Chasmaporthetes* also point to a close relationship between these taxa.

By contrast, the latest Miocene/early Pliocene *Euryboas* from Langebaanweg is less well suited to the role as structural ancestor of *Chasmaporthetes*, and a direct phylogenetic connection between these taxa is, at the very least, highly improbable. On the other hand, the Langebaanweg *Euryboas* is in every respect ideally suited to be the ancestor of the late Pliocene/early Pleistocene *E. bielawskyi* of Europe.

The earlier view that *Chasmaporthetes* and *Euryboas* evolved independently, with the latter being an essentially African genus which also spread into southern Europe (Hendey 1975), is here maintained.

In considering the origins and relationships of *Chasmaporthetes* and *Euryboas*, another important species which has to be taken into account is '*Hyaena*' *borissiaki* from the Pliocene of Moldavia in the Soviet Union (Khomenko 1932). De Beaumont (1967) believed it to be an intermediate

between *Lycyaena* and various species now assigned to *Chasmaporthetes* and *Euryboas*. More recently Galiano & Frailey (1977: 9) noted that it has characters in common with both these genera, but concluded that '*H.* *borissiaki* 'appears to be referable to *Chasmaporthetes sensu stricto*'.

'*H.* *borissiaki* is evidently broadly contemporary with the hyaenids from Langebaanweg, although the actual ages of the Moldavian and South African species are not known. The relative ages of these hyaenids could be crucial to the interpretation of their relationships. '*H.* *borissiaki* has characters in common with both *Adcrocuta australis* and the *Euryboas* from Langebaanweg. For example, both '*H.* *borissiaki* and the *Euryboas* have straight cheektooth rows and jaws, while their cheekteeth are comparable in both size and morphology. On the other hand, '*H.* *borissiaki* resembles *A. australis* in cheektooth morphology, most significantly in having a reduced P⁴ protocone. In this respect, and in the occasional presence of P₁, it is also similar to *A. eximia variabilis*.

In terms of the interrelationships postulated here, '*H.* *borissiaki* may be visualized either as an intermediate between *A. eximia variabilis* and *Chasmaporthetes*, or as an early *Euryboas* which was not conspecific with the Langebaanweg species. The first of these alternatives is perhaps the more likely and, following Galiano & Frailey (1977), '*H.* *borissiaki* is here tentatively regarded as an early *Chasmaporthetes*.

Nevertheless, the similarities to *Euryboas* are striking and, as a further alternative, *Chasmaporthetes? borissiaki* may be interpreted as the species from which both *Euryboas* and *Chasmaporthetes* were derived. This possibility would be strengthened should it transpire that *C.? borissiaki* predates the Langebaanweg *Euryboas*. In the case of this alternative, the stem form might either have been *Lycyaena*, as De Beaumont (1967) suggested, or *Adcrocuta*, as indicated above.

While the phylogenetic position of *C.? borissiaki* is uncertain, it is clearly a species of great significance in the matter of 'hunting hyaena' interrelationships.

Judged on available evidence the hypothetical *Adcrocuta-Chasmaporthetes* transition took place in Asia some time between the late Miocene and early Pleistocene. Members of this lineage dispersed eastwards into North America by way of the Bering Land Bridge, and westwards into Europe and perhaps also Africa.

A problem which arises in connection with this theory concerns the age of *C. kani*, which was given as 'Early Pleistocene' by Galiano & Frailey (1977: 2). If this was indeed the case, then *C. kani* must be younger than at least some of the European and North American specimens assigned to *Chasmaporthetes*, even though it is more primitive in an evolutionary sense. Either *C. kani* is older than Galiano & Frailey suppose, or it was a conservative species, little different from a Pliocene form from which late Pliocene/early Pleistocene European and North American *Chasmaporthetes* must have been derived. In other words, the latter are likely to have stemmed from a *C. kani*-like

ancestor of Pliocene rather than early Pleistocene age. *C.?* *borissiaki* could possibly be the species in question.

The actual dates when *Chasmaporthetes* first appeared in Europe and North America have yet to be firmly established. If the Plio/Pleistocene boundary is taken at about 2 m.y. before present, then migration to North America must have been during the late Pliocene, since *Chasmaporthetes* is recorded from the 'early Blancan' (Repenning 1967), which is of late Pliocene age (Kurtén 1971). The Olivola and Senéze faunas of Europe, which include *C. lunensis* (Galiano & Frailey 1977), date from the latter part of the Villafranchian (Kurtén 1968), which postdates the early Blancan. The migration to Europe may thus have been later than that to North America.

The ranges of *Chasmaporthetes* and *Euryboas* overlap both temporally and geographically in Europe and, in view of their shared characteristics, they may well have competed with one another. It is not known which of the two taxa survived longest in Europe, but that honour may go to *Chasmaporthetes*.

The situation in Africa is somewhat obscure, the basic problem being to which of the two genera material from the Transvaal caves and undescribed specimens from east Africa (e.g. Howell & Petter 1976) belongs. The best

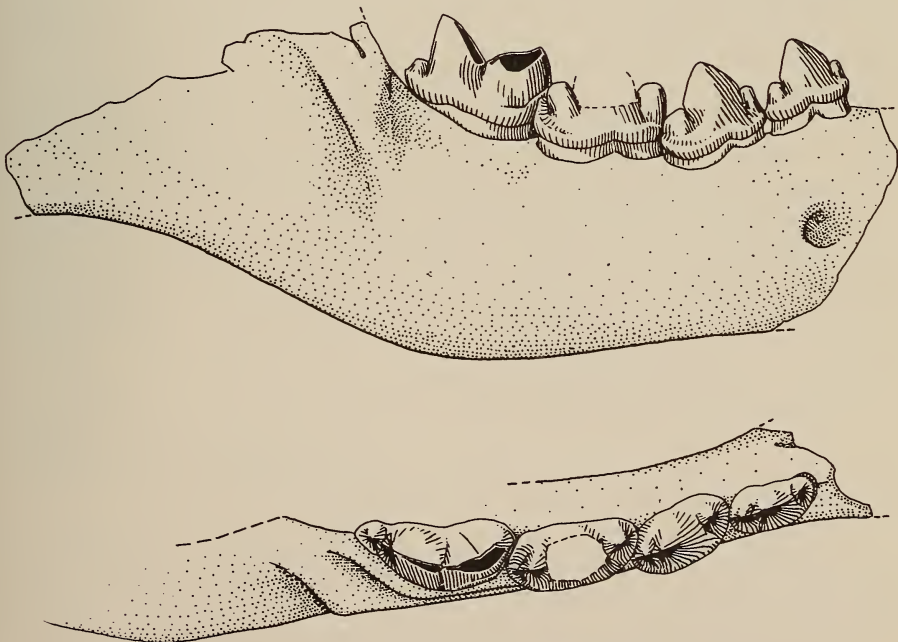


Fig. 10. Lateral and occlusal views of *Chasmaporthetes nitidula* hemimandible from Swartkrans (Transvaal Museum SK14005). (80% of natural size.)

TABLE 4

Some characteristics of the lower teeth and jaws in *Adcrocuta*, *Chasmaporthetes* and *Euryboas*

	late Miocene <i>Adcrocuta eximia</i> <i>variabilis</i> (China)	latest Miocene/ early Pliocene <i>Adcrocuta australis</i> (Langebaanweg)	'Early Pleistocene' <i>Chasmaporthetes</i> <i>kani</i> (China)	late Pliocene <i>Chasmaporthetes</i> <i>lunensis</i> (Saint-Vallier)
Shape of jaw (ventral view)	straight (?or curved)	straight or curved	?	curved
Shape of cheektooth row (occlusal view)	curved	curved	curved	curved
Canine height	low	low	?	low
Shape of P ₃	rectangular	rectangular	ovate	ovate
Anterior accessory cusps of P ₂ and P ₃	sometimes absent	sometimes absent	sometimes absent	present
M ₁ talonid	bicuspid or unicuspid	unicuspid	unicuspid	unicuspid

represented of the later African forms is '*Euryboas*' *nitidula* from Swartkrans, which Galiano & Frailey (1977) believe may be a *Chasmaporthetes*. In their view referral to this genus would be more certain if 'the condition of P¹ and the degree of curvature of the tooth rows' were known (Galiano & Frailey 1977: 9). The condition of P¹ is still not known, although it may well have been absent, but the tooth rows, and jaws, are curved (Fig. 10), as in *Chasmaporthetes*. The case for referral of '*E.*' *nitidula* to *Chasmaporthetes* is thus strengthened and the Swartkrans species is here recognized as *Chasmaporthetes nitidula*.

The date when *Chasmaporthetes* entered Africa is not known, but it may have postdated its entry into Europe. That unit of the Swartkrans fauna which includes *C. nitidula* dates back about 1.5 m.y. (Vrba 1976), which makes it one of the youngest records of the genus, another being the *C. ossifragus* from Inglis IA in Florida (Webb 1974). There is thus evidence that in Africa *Chasmaporthetes* survived longer than *Euryboas*.

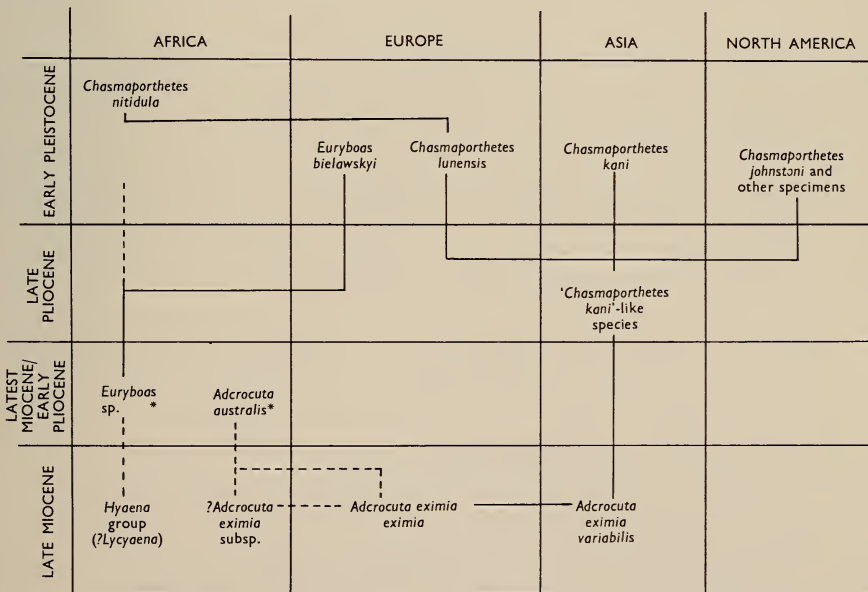
Present indications are that *Chasmaporthetes* was the more widespread, and ultimately also the more successful of the two 'hunting hyaena' genera. It was, in fact, the most widely distributed of all hyaenids, having occurred over much of North America as well as the Old World.

The interrelationships of *Adcrocuta*, *Chasmaporthetes* and *Euryboas* as interpreted here are summarized in Figure 11, while some of their more significant characters from a phylogenetic point of view are listed in Table 4. *Chasmaporthetes? borissiaki* is omitted owing to the uncertainties surrounding it.

The discovery of additional specimens of different ages and from different geographical locations, and accurate dating of specimens already known, should allow testing of the opinions expressed in this paper. The recent dis-

late Pliocene <i>Chasmaporthetes johnstoni</i> (Ta Canyon)	early Pleistocene <i>Chasmaporthetes ossifragus</i> (Inglis IA)	early Pleistocene <i>Chasmaporthetes nitidula</i> (Swartkrans)	latest Miocene early Pliocene <i>Euryboas</i> sp. (Langebaanweg)	late Pliocene <i>Euryboas bielawskyi</i> (Roccaneyra)
curved	curved	curved	straight	straight
curved	curved	curved	straight	straight
?	?	low	high	high
ovate	ovate	ovate	rectangular	rectangular
present	present	present	absent	absent
unicuspid	unicuspid	unicuspid	bicuspid	unicuspid

coveries at Langebaanweg and identification of the first Asiatic *Chasmaporthetes* have already clarified the situation to some extent and no doubt more relevant material will still come to light.



*Langebaanweg species

Fig. 11. Tentative phylogeny of *Euryboas* and *Chasmaporthetes*.

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Some characteristics of the lower teeth and jaws in *Adcrocuta*, *Chasmaporthetes* and *Euryboas*.

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Canine height	low	low	?	low	low	?	low	high	high
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Anterior accessory cusps of P ₂ and P ₃	sometimes absent	sometimes absent	sometimes absent	present	present	present	present	absent	absent
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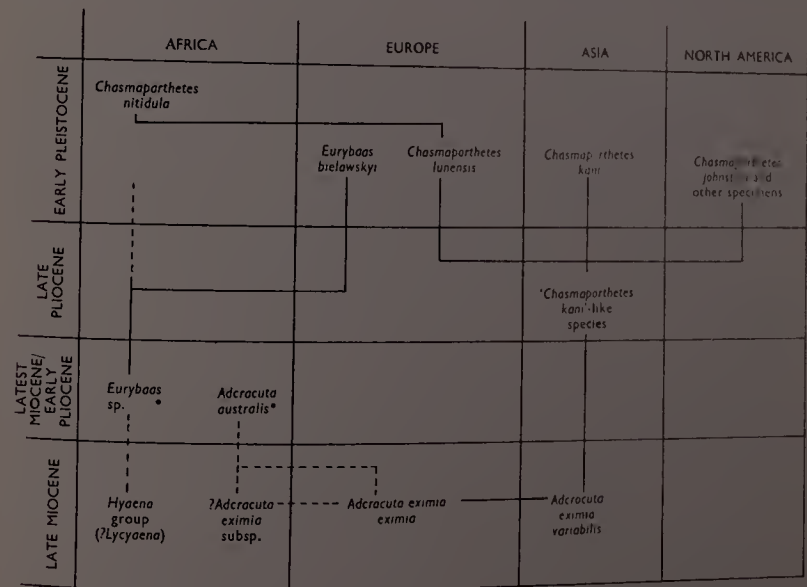
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